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# Spatial patterns of tree yield explained by endogenous forces through a correspondence between the Ising model and ecology

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**Spatial patterning of periodic dynamics is a dramatic and ubiquitous ecological phenomenon arising in systems ranging from diseases to plants to mammals. The degree to which spatial correlations in cyclic dynamics are the result of endogenous factors related to local dynamics vs. exogenous forcing has been one of the central questions in ecology for nearly a century. With the goal of obtaining a robust explanation for correlations over space and time in dynamics that would apply to many systems, we base our analysis on the Ising model of statistical physics, which provides a fundamental mechanism of spatial patterning. We show, using 5 y of data on over 6,500 trees in a pistachio orchard, that annual nut production, in different years, exhibits both large-scale synchrony and self-similar, power-law decaying correlations consistent with the Ising model near criticality. Our approach demonstrates the possibility that short-range interactions can lead to long-range correlations over space and time of cyclic dynamics even in the presence of large environmental variability. We propose that root grafting could be the common mechanism leading to positive short-range interactions that explains the ubiquity of masting, correlated seed production over space through time, by trees.**

ecology | Ising model | universality | physics | plant science

**S**patial dynamics and patterning are central issues in many fields of science (1–5), including ecology, where the interface of theory and data has the potential to provide unique insights into emergent behaviors and underlying causes (6). Among the most dramatic emergent behaviors in ecology is “masting” of perennial plants, in which individual fruit or seed production varies through time and is correlated across space (7–9). In some tree species, individual production is primarily described by a two-cycle alternating of years of high and low production (10, 11). Patterns of spatially synchronized two-cycles are of great interest as they are found not only in trees but also in systems ranging from childhood diseases to small mammals (12–17).

Determining aspects of process from pattern is a fundamental problem because setting up experiments or gathering observations on relevant temporal and spatial scales is logistically challenging, so experimental treatments have been limited to microcosms (17). Here, we take advantage of an agricultural system that is on a much larger spatial scale than typically available experimentally (11). This kind of agricultural dataset then leads to the challenge of developing a modeling approach focused on the relevant details in a very large complex system. Even the first step of developing appropriate measures and expectations for spatial synchrony has proved to be a difficult challenge (17).

There are two approaches to explaining spatiotemporal patterns in fruit production. One could ask, What are the advantages from an evolutionary standpoint? Or somewhat differently one could ask, What are the proximate mechanisms, both from biological and from modeling frameworks, that lead to synchrony in reproduction by plants at different spatial scales (8)? We take the latter approach since the behavior of the trees in the agricul-

tural systems we study is not the subject of direct selection but perhaps reflects evolutionary history. Our motivation is to use modeling and data analysis to infer the plausibility of potential proximate mechanisms that could then be further analyzed.

The basis of our work is that the ubiquity of spatiotemporal patterning in tree fruit production implies that there should be relatively generic, detail-free explanations. It is also plausible that direct interactions are short range, yet correlations are observed over longer spatial scales. Finally, a deterministic approach is not sensible as large environmental noise typically affects both agricultural systems and more general ecological systems. The search for this kind of robust system-independent description leads us to ideas from statistical physics.

Approaches from statistical physics have provided insights into how local behavior and short-range interactions can generate emergent spatial patterns ranging from desertification (18–20) to schooling behavior of fishes and flocking behavior of birds (21, 22), but have not previously been used to understand patterns and causes of spatial synchrony in cyclic dynamics in data from population biology. More generally, statistical physics seeks to explain emergent behavior, such as scale-invariant pattern formation, in large (high-dimensional) complex systems (3–5, 18, 19, 23, 24). A key theme is critical phase transitions between order and disorder (3–5, 23), which lead to identifiable long-range spatial patterns and other characteristic behaviors. Identifying these

## Significance

**Explaining correlations across space of cyclic dynamics in ecology is a fundamental challenge. We apply ideas from statistical physics, originally used to explain the behavior of magnets, to a dataset on yield from pistachio trees, obtaining a robust description and potential explanation for the generation of spatial correlations in cyclic dynamics. These results suggest looking for mechanistic underpinnings at the level of interactions between neighboring trees that lead to spatial correlations in dynamics and a surprising correspondence between the descriptions of physical phenomena, magnetization, and ecological dynamics. This work demonstrates with data, and not just models, that correlations in cyclic dynamics can be generated from local interactions and dynamics even in a very noisy ecological system.**

Author contributions: A.E.N., T.S.R., P.H.B., J.M., and A.H. designed research; A.E.N. and T.S.R. performed research; A.E.N. and T.S.R. analyzed data; and A.E.N., T.S.R., P.H.B., J.M., and A.H. wrote the paper.

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characteristic signals in data can then be used to infer properties of underlying mechanisms that provide a parsimonious explanation for observed behavior. We previously used this approach to demonstrate, within a modeling framework, how long-range (i.e., power-law decaying) spatial correlations in systems of coupled ecological oscillators are explained by the Ising model, which is a canonical model of statistical physics (24).

### Ising Model Description of Spatial Ecological Dynamics

The Ising model is a standard model in statistical physics for understanding how scale-invariant correlations emerge in a model-independent, or universal, way at critical transitions (3–5). Our previous work on Ising universality of critical transitions in the spatial synchrony of ecological population models uses the isotropic Ising model on a 2D lattice (24). Since the vertical and horizontal spacing of trees differs in our study area, here we use the anisotropic Ising model in which the horizontal couplings  $J_H$ , between sites in neighboring columns, and the vertical couplings  $J_V$ , between sites in neighboring rows, may be different. The “spin” at site  $x$  in the anisotropic 2D Ising model is a binary random variable,  $s_x \in \{-1, 1\}$ , and the probability of any configuration of spins, denoted  $\{s_x\}$ , is given by the Gibbs distribution

$$P(\{s_x\}) \propto \exp(-\mathcal{H}(\{s_x\})), \quad [1]$$

where  $\mathcal{H}(\{s_x\})$  is a so-called “reduced energy function” that can be written as

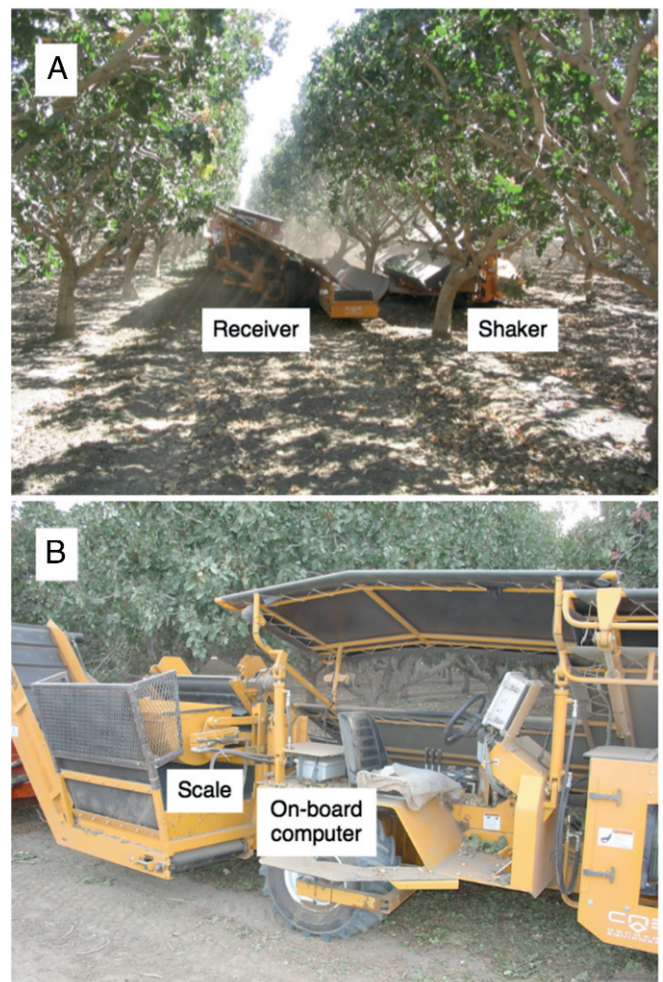
$$\mathcal{H}(\{s_x\}) = -J_H \sum_{\langle xy \rangle_H} s_x s_y - J_V \sum_{\langle xy \rangle_V} s_x s_y - h \sum_x s_x \quad [2]$$

with  $\langle xy \rangle_H$  and  $\langle xy \rangle_V$  denoting the sets of all horizontal neighboring spins and all vertical neighboring spins, respectively. The third term in the expression describes the effect of an external magnetic field  $h$  acting on all spins. The overall negative sign means that the reduced energy is lower (higher) when neighboring spins are more (less) aligned. Because the probability of any given configuration of local spin states over the lattice is given by the Gibbs distribution, configurations with a high degree of local alignment, or ordered configurations, are typical if both  $J_H$  and  $J_V$  are sufficiently large. Alternatively, if the external field  $h$  is large, the spins will be aligned with the field. Low levels of local alignment, or disordered configurations, are typical if  $J_H$ ,  $J_V$ , and  $h$  are sufficiently small. Critical transitions between order and disorder occur for  $h = 0$  and intermediate values of  $J_H$  and  $J_V$ . In the current context of masting trees, each spin in the Ising model represents the phase of production of a tree. If  $s_x = 1$ , the tree at site  $x$  produces a large crop in even years and vice versa for  $s_x = -1$ . Thus, the spin variables are related to first differences in yearly production (*Materials and Methods*). The couplings  $J_H$  and  $J_V$  represent endogenous interactions that favor phase locking and the field  $h$  represents the synchronizing effect of global exogenous forces such as a weather event (Moran effect). Thus, the external field  $h$  is typically a random function of time.

In the context of the Gibbs distribution, ordered (synchronized) states can arise either from strong couplings ( $J$ ) or strong fields ( $h$ ); however, within a dynamical Ising model it may be possible to distinguish these alternatives. If an ordered state in a large system arises quickly from a disordered state, it must be due to a strong field  $h$  rather than strong couplings because the ordering effect of strong couplings requires long times to propagate over large distances.

### Results

Observations of masting based on individual production of over 6,500 trees over a 5-y period in a commercial pistachio (*Pistacia vera*) orchard (11, 25) (Figs. 1 and 2) provide a dataset that is

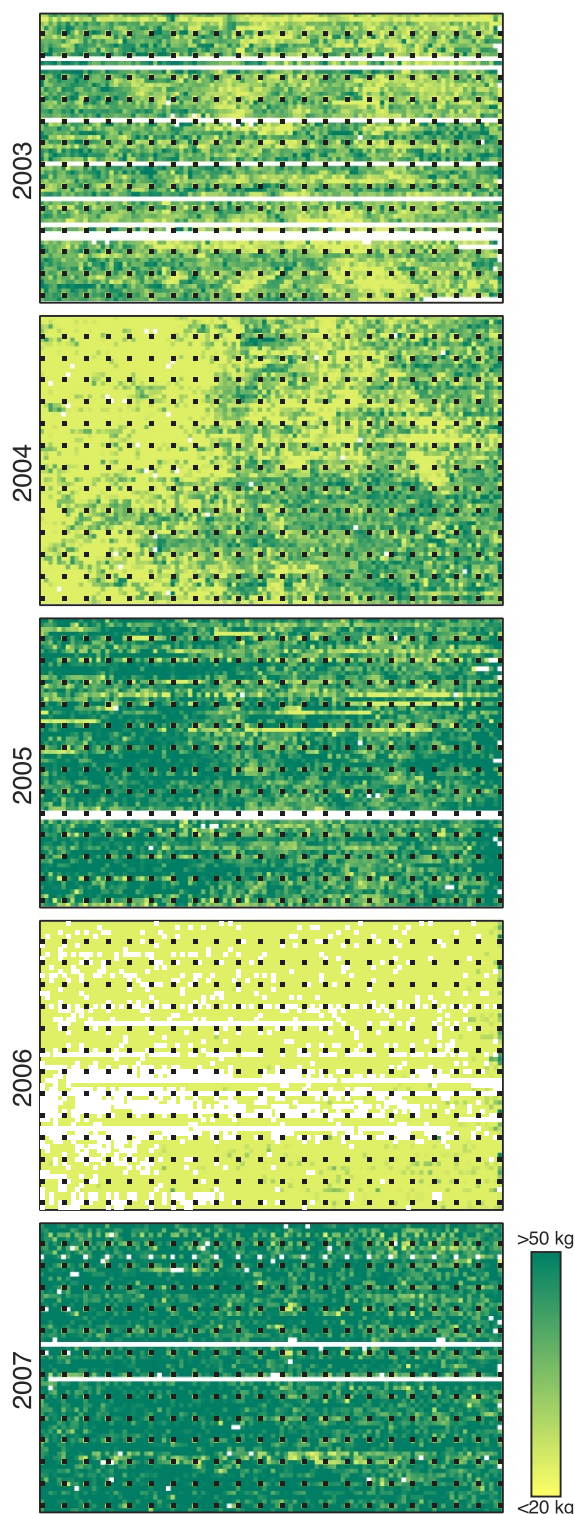


**Fig. 1.** Obtaining high-resolution spatial data on individual pistachio tree production. The Lost Hills orchard in Kings County, CA is planted on a precise grid with 5.2 m between columns and 6.4 m between rows. (A) Annual harvesting is fully automated and proceeds down the rows (Movie S1). The “shaker” shakes each female tree near the resonance frequency of the individual fruits on their small stems. The “receiver” collects the fallen pistachios. (B) The receiver was equipped with an electronic scale and on-board computer (25), allowing for accurate measurement of the production of  $N = 6,710$  individual female trees occupying a 9.3-hectare study area (Movie S2).

distinguished by its size and underlying homogeneity, presenting a unique opportunity for using ideas from statistical physics to analyze an ecological system. This system is at least an order of magnitude larger than laboratory microcosms (26, 27) and much more homogeneous than epidemiological datasets (16), which have provided much of the basis for understanding spatiotemporal dynamics in ecology. By using ideas from statistical physics to analyze the pistachio dataset, we can begin to assess the relative importance of exogenous forces, such as the number of winter chilling hours for trees, the amount of precipitation falling during the spring flowering season, and irrigation and other management practices, from endogenous local forces, such as chemical signaling, trophic interactions with microorganisms, and root grafting (28, 29).

We do note one potential complication in simply relating nut production to the state of the tree that is important in our analysis. Yield from an individual tree in a year is a function of the state of the tree (e.g., carbon storage) when it awakes from dormancy and environmental factors during flowering and fruit





**Fig. 2.** Individual pistachio tree production within study area. Color bar indicates production of individual female trees in each year. Black squares indicate the location of male trees, which do not bear fruit. White squares indicate missing data. The homogeneity of the spatial pattern in 2005–2007 indicates that the exogenous forcing of the Moran effect dominates endogenous forces in regulating production. Indeed, this is the expected pattern of production given that pistachio tree genetics, soil conditions, and management practices are highly uniform across our 9.3-hectare study area. This makes the multiscale heterogeneities observed in 2003 and 2004 surprising. Rather than being entrained to large-scale regional growing conditions, the emergent spatial patterns in 2003 and 2004 indicate that endogenous forces dominate the Moran effect in producing spatial correlations.

development. Some of the environmental factors, which affect flowering, also affect the future state of the tree, as reduced flowering or pollination means fewer resources are required to meet vegetative and reproductive needs and more are available for storage and use the subsequent year (30). But other factors, such as those producing "June drop" (31) or nut flower bud abscission, reduce yield but do not change the state of the tree as much as if the nuts were to develop and be harvested (32). Thus, in any given year, the state of the tree is a random variable which is a function of the state of the tree the year before, and the yield from a tree can be thought of as a function of the state of the tree and a random component which has large but not complete spatial correlation among all of the trees.

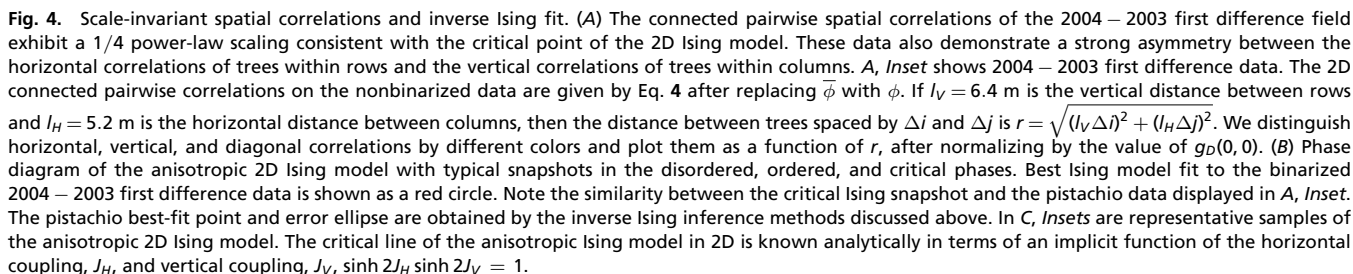
Given the high degree of underlying homogeneity in soil and moisture conditions as well as the use of a single cultivar in the study area and its small spatial extent relative to the typical length scales over which significant variation tends to be found in environmental conditions, the a priori expectation for pistachio production in the study area would be spatially uniform and highly synchronized by long-range, exogenous forces—the Moran effect (33). This is the case for 2005–2007 (Fig. 2). In addition, total study area production in 2005–2007 is strongly correlated with county and regional production (Fig. 3). In the context of the Ising model, a strong field  $h$  is present at least in 2006–2005 and perhaps subsequent years. Additionally, the June drop phenomenon means that the observation is a function of both the state of the tree at the beginning of the growing season and an additional random factor. Nonetheless, the entrainment of local orchard-level production to regional production and ultimately to climatic conditions is a particularly clear signal of a Moran effect dominating the system. In principle, strong local couplings might also produce the synchrony clearly observed in the 2006–2005 orchard data. However, since synchrony is absent in 2003–2004, there is insufficient time for local interactions to synchronize the whole orchard.

This baseline expectation of complete synchrony makes the observed deviations in 2003 and 2004 especially surprising. In our analysis of these 2 y, we find highly heterogeneous spatial patterns in the production data (Fig. 2), with clusters of synchronized production on many different length scales in the study area. Simultaneously, we observe a desynchronization of local production from the regional average (Fig. 3). Thus, there is no strong global forcing and, in the Ising setting, the field  $h$  is weak or absent. The fractal-like structure of the 2003 and 2004 spatial patterns in pistachio production is strikingly similar to spatiotemporal patterns previously found in theoretical predictions for the behavior of locally coupled noisy two-cycle ecological oscillators (24), in which the emergent fractal patterns were shown to be model independent and described by the 2D Ising universality class of statistical physics. The spatiotemporal use of the pistachio system has all of the ingredients required to observe Ising-like behavior: The pistachios are planted on a 2D grid; the individual production of alternate bearing female trees oscillates in a noisy nonlinear two-cycle (10, 30); and there are potential sources of positive local coupling among neighboring trees, such as root grafting.

This motivates us to estimate the same first difference statistics in the pistachio data that were used to map ecological population dynamics onto the 2D Ising model in our theoretical work (24). Calculating pairwise correlations in the “2004 – 2003” first difference field, we find a result which displays long-range correlations (Fig. 44) significantly different from expectations for an uncorrelated random spatial process or the kind of patchiness described in ref. 18. Indeed, we find strong evidence of long-range correlations in the pistachio data consistent with the 2D Ising critical point where the exponent of the power law decay is  $1/4$ , as seen in the data. Additional evidence of this mechanism is obtained by explicitly demonstrating that a critical point of a 2D anisotropic Ising model, a model with only two free parameters,







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$$g_D(\Delta i, \Delta j) = \frac{1}{2N_{\Delta i, \Delta j}} \sum_i \sum_j \bar{\phi}_{ij} \bar{\phi}_{i+\Delta i, j+\Delta j} \quad [4]$$

skipping any terms in which the value of  $\bar{\phi}_{ij}$  or  $\bar{\phi}_{i+\Delta i, j+\Delta j}$  is undefined and denoting by  $N_{\Delta i, \Delta j}$  the total number of terms in the sum.

On the modeling side, for any given values of  $J_H$  and  $J_V$ , we use the Wolff algorithm (47) to draw 10,000 independent samples of the anisotropic 2D Ising model on a  $154 \times 151$  lattice with free boundary conditions. The size of this lattice is equal to the size of the isolated orchard subplot that contains the study area. We calculate the 2D connected pairwise correlations within the study area just as in Eq. 4. Repeating this procedure for all 2D Ising samples gives us the mean value for each pairwise correlation,  $g_M(\Delta i, \Delta j)$ , and the SD,  $\sigma(\Delta i, \Delta j)$ .

There are other modeling assumptions of ecological interest. First, we cannot ignore the male trees. In fact, the fit presented here assumes that the local interactions of male and female trees are identical. This result suggests that levels of the unidentified endogenous signal in male trees also oscillate in a noisy nonlinear two-cycle and that the local coupling (root grafting is one example) is independent of sex. Second, simulations restricted to the  $66 \times 106$  study area generate large systematic deviations from the observed power-law correlations in Fig. 4A. A good fit is obtained only when we simulate the 2D Ising model on the full  $154 \times 151$  grid of the surrounding orchard subplot, which is bounded by wide access roads, on all four sides, that inhibit root grafting with trees at the boundaries of neighboring subplots. A cutoff to the power-law correlations in small systems is a known property of the 2D Ising model that, in this context, provides additional evidence that the observed scale invariance of pistachio production in 2003

and 2004 is indeed an emergent phenomenon regulated by endogenous interactions of each individual tree with its four nearest neighbors.

The county data summarized in main text and **Datasets S1–S3** were obtained from standardized reports made publicly available by Agricultural Commissions of Fresno, Kern, Kings, and Tulare Counties (Fresno, [www.co.fresno.ca.us/departments/agricultural-commissioner/crop-report-history](http://www.co.fresno.ca.us/departments/agricultural-commissioner/crop-report-history); Kern, [www.kernag.com/caap/crop-reports/crop-reports.asp](http://www.kernag.com/caap/crop-reports/crop-reports.asp); Kings, [www.countyofkings.com/departments/general-services/agriculture-department-measurement-standards/ag-services/crop-reports-1941-2013/test](http://www.countyofkings.com/departments/general-services/agriculture-department-measurement-standards/ag-services/crop-reports-1941-2013/test); and Tulare, [agcomm.co.tulare.ca.us/default/index.cfm/standards-and-quarantine/crop-reports1/crop-reports-2000-2010](http://agcomm.co.tulare.ca.us/default/index.cfm/standards-and-quarantine/crop-reports1/crop-reports-2000-2010)). All measurements of individual tree yield are rounded to the nearest pound. Row 0, column 0 references the female tree in the far southwest corner of the study area. The term “-1” indicates a missing value and “-2” indicates a male tree.

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